

ZOOLOGIA 92

“Systematics and phylogeny: theoretical,
morphological, biochemical and
biogeographical aspects”

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ABSTRACTS

MAIN LECTURES

Olivier Rieppel (Chicago): The relation of cladistics to evolutionary theory.

“A false analogy has been drawn between taxonomic groups and individuals... This analogy led to the belief that a relationship exists between groups analogous to the genealogical relationship between individuals” (J.S.L. Gilmour, 1940, in Huxley, J. [ed.]: *The New Systematics*, p. 471). Cladistics constitutes an empirical, rational and non-arbitrary “discovery procedure” (G. Nelson) for the reconstruction of an inclusive hierarchy of “groups within groups” (Darwin). Homology becomes unequivocally defined only if tied to monophyly, i.e. synonymized with “synapomorphy”. The test of congruence provides the clue to the level of inclusiveness at which topological relations of similarity are homologous. This methodological procedure is justified with reference to “Gilmour-naturalness”, requesting maximum information content for natural classifications. Taxic homology defines inclusive relations: a mammal is not only a representative of the Mammalia, but also of the Amniota, Tetrapoda, Gnathostomata, Vertebrata etc. The inclusive hierarchy of “groups within groups” is related to the concept of common ancestry, but is not explained by Darwinian mechanisms of evolutionary change which address the exclusive hierarchy of ancestors and descendants (a descendant cannot be part of its ancestor, but must follow its ancestor in time and space). No “discovery procedure” is available to objectify ancestor – descendant relationships, which remain elusive in terms of empiricism and logics. From this results an incompatibility yet complementarity of pattern reconstruction (in cladistic terms) and process explanation (in Darwinian terms). Alternatives to pluralism in comparative biology can only be “Radical Solutions to the Species Problem”. One is to view Darwinism as a “falsified” theory, and to treat causal mechanisms of macroevolutionary change as a “black box” (G. Nelson). The other is to view species (and, by implication, supraspecific taxa) as individuals (M.T. Ghiselin), which deprives speciation and macroevolutionary change of underlying lawfulness.

J. Géry (Sarlat): Rapports entre l'écologie et la systématique chez certains Poissons characiformes néotropicaux.

La taxonomie, l'écologie et la biogéographie sont inextricablement liées, et tout travail de taxonomie, même au stade de la description d'espèce, doit tenir compte, entre autres, des notions de patrons de distribution, de niche, de vicariance, etc., ainsi que de sympatrie et d'allopatricie, pour lesquelles Mayr et al. avaient publié un tableau de discrimination fort pratique qui est rappelé ici. C'est pour toutes ces raisons que j'avais proposé, il y a 30 ans, d'appeler cet ensemble de démarches «l'éco-taxonomie», sans grand succès d'ailleurs.

Cette conférence traite de quelques cas relevant de ces idées:

I. Dans une première partie, les résultats d'une étude sur la faune characoïde (Poissons ostariophyses) d'une partie de la Guyane sont présentés sous forme d'un dendrogramme, obtenu par groupement d'un tableau de similitude des stations qui concernent la faune d'un grand fleuve côtier, le Maroni, à plusieurs hauteurs, d'une part, et la faune de plusieurs petits cours d'eau, les uns appartenant à ce même bassin hydrographique, les autres à un autre bassin éloigné de 250 km à vol d'oiseau.

Le dendrogramme montre que les stations se groupent non pas suivant la géographie, mais suivant l'écologie, c'est-à-dire que la faune des petits cours d'eau, même éloignés, a un coefficient de similitude plus proche que celle des fleuves, comme si l'écologie jouait un plus grand rôle que la géographie dans la répartition actuelle des espèces. Un tel résultat, intuitivement attendu, ne doit pas faire négliger le rôle plus ancien qu'a dû jouer l'histoire physique (géographique) de cette partie relativement stable de l'Amérique du Sud. Cette étude a permis également de tester quelques modèles utilisés en écologie quantitative (espèces constantes et accessoires, modèle d'Arrhénius où le nombre d'espèces est proportionnel à la surface du bassin versant), et de comparer la faune characoïde des Guyanes avec la faune pisciaire de Côte d'Ivoire beaucoup moins riche (comme d'autres bassins africains sont aussi beaucoup moins riches que des bassins néotropicaux équivalents).

II. Une deuxième étude met mieux en évidence le rôle de l'histoire dans la répartition des espèces, en s'intéressant à un genre particulier et probablement très ancien, *Pseudochalceus*, dont la distribution des 5 espèces actuellement connues est restreinte à quelques fleuves côtiers du Nord-Est et du Sud-Est de l'Amérique du Sud, sans qu'aucune forme analogue ait été récoltée entre ces deux régions.

Les espèces offrent deux types de coloration. L'un, présent à la fois en Equateur et dans le Sud-Est du Brésil, est particulièrement bradytélétique si on admet que sa présence aux deux extrémités du continent n'est pas fortuite, mais qu'elle résulte de l'histoire géologique depuis la fin du Crétacé. En Equateur, pratiquement aucune dérive génétique n'a été découverte dans les quelques stations étudiées, tandis qu'au Brésil, les populations, dont il a été possible d'étudier quelques échantillons, ont atteint le niveau racial, au plus subsppécifique. L'autre type, connu seulement du Nord-Est où il habite les fleuves côtiers de Colombie et de l'Equateur, s'est un peu diversifié et représente apparemment trois espèces distinctes. Aucune explication n'a été donnée sur ce comportement évolutif différentiel. En particulier, on ne connaît pas l'avantage sélectif de tel ou tel patron de coloration.

III. Dans le même ordre d'idées, on n'a encore aucune idée sur les pressions de sélection qui agissent sur les petits Poissons de surface *Carnegiella*, purement amazoniens ceux-là, et bien connus sous les noms de Poissons-hachettes ou Poissons-volants. Ils présentent un polymorphisme qui peut être réduit, par une analyse des populations, à deux types, se distinguant par la fasciature de la carène typique de cette famille (les Gasteropelecidae), et par des différences statistiques pour trois caractères: le rapport de la hauteur du corps et du coracoïde sur la longueur standard, et le nombre des rayons ramifiés de la nageoire anale.

L'analyse aboutit, à titre d'hypothèse, à distinguer deux formes, qui seraient peut-être sympatriques au sens large (parapatriciques?) dans certains petits cours d'eau de l'Amazonie supérieure et, peut-être, du Rio Negro. Les échantillons de ces régions montrent certains caractères intermédiaires et une variabilité augmentée, ce qui conduit à penser qu'il s'agit de formes en voie de spéciation, encore capable de s'hybrider lorsqu'elles viennent à se rencontrer. Il a été possible de bâtir des cartes de distribution, fondées sur les moyennes des caractères étudiés, sans qu'on puisse trouver les facteurs écologiques qui ont amené une telle distribution. Toutefois les deux types semblent se

distribuer au nord et au sud de l'Amazonie, et il n'est pas exclu que la formation géologique du bassin ait pu agir sur cette répartition.

IV. La distribution géographique de certains caractères, présents ou absents dans des groupes très voisins, peut aussi s'expliquer par ces mêmes facteurs, écologiques et (ou) géographiques: c'est ainsi que la répartition des nombreuses espèces des genres voisins *Hemigrammus* et *Hyphessobrycon*, petits Tétràs connus de tous les aquariophiles, qui ne se distinguent classiquement que par la présence ou l'absence, respectivement, d'écailles sur la nageoire caudale, semble répondre à un schéma d'ensemble: les espèces à caudale écaillée sont relativement plus nombreuses dans la région guyano-amazonienne. Le même schéma se retrouve dans la répartition respective des *Moenkhausia* et des *Astyanax*.

D'autres cas peuvent être envisagés dans cette optique «éco-taxonomique», en particulier la coloration semblable des «Tétràs néons» du genre *Paracheirodon*, vicariants habitant l'Amazonie supérieure et le Rio Nègre, deux bassins dont les biotopes sont assez différents, et le «groupe *rhodostomus*» ou «nez-rouges», encore des espèces bien connues des aquariophiles, dont le pattern de distribution pose la même alternative entre facteur écologique et facteur historique.

François M. Catzeflis (Montpellier): Molécules et morphologie en reconstruction de phylogénies: que choisir?

Reconstruire une phylogénie d'organismes signifie situer ceux-ci dans l'espace taxonomique (systématique) et temporel (paléontologie, horloge moléculaire). Quelle que soit l'école de pensée (néo-darwinienne, phénétique, cladistique) utilisée en cette matière, il s'avère que ce sont les caractères portés par les organismes qui forment le matériau de base pour reconstruire l'histoire évolutive des êtres concernés. Ces caractères ont longtemps été exclusivement morphologiques, basés sur l'anatomie comparée et l'embryogenèse. Une des difficultés majeures du traitement de caractères morphologiques, de l'avis des spécialistes, est de sélectionner avant tout la variation héritable, c'est-à-dire d'exclure les caractères (trop) soumis aux conditions du milieu ou dépendant de l'âge des individus. L'emploi de caractères moléculaires, telles les séquences des protéines (qui appartiennent aussi au phénotype !) ou des acides nucléiques ADN et ARN, renforce la probabilité de traiter des variations héritables. Actuellement, on peut dire qu'il n'y a pas de différence fondamentale, dans le cadre de reconstructions de phylogénies, entre l'emploi des molécules ou de la morphologie, à condition qu'un certain nombre de précautions soient prises afin de diminuer l'homoplasie et d'assurer l'homologie des structures comparées.

Quoi qu'il en soit, la difficulté majeure apparaît après avoir découvert et observé les caractères (et leurs divers états), lorsqu'il s'agit de traiter ceux-ci pour reconstruire des arbres évolutifs.

Plusieurs approches existent aujourd'hui, qui devraient être considérées en parallèle plutôt qu'en compétition exclusive. Chacune de ces approches (distances, parcimonie, maximum de vraisemblance, compatibilité) a ses faiblesses et qualités, et la plus grande difficulté revient à départager l'homoplasie (bruit de fond) des informations phylogénétiques. Ainsi, le maximum de parcimonie, considéré encore récemment comme «le meilleur» traitement de séries de nombreux caractères, apparaît comme fallacieux dans certains cas, notamment ceux où de longues branches évolutives chargées d'autapomorphies ne sont représentées que par un taxon.

L'aspect temporel de l'arbre évolutif provient directement de la lecture et de l'interprétation du registre fossile, et indirectement de l'emploi du concept de l'horloge moléculaire. Cette dernière n'est pas universelle, c'est-à-dire que d'une part différents compartiments du génome évoluent à différentes vitesses chez le même organisme, et d'autre part, une même [= homologue] structure moléculaire peut évoluer à différents taux chez différents organismes, même étroitement apparentés. Comprendre l'étendue de la variabilité de ces deux aspects est fondamental pour pouvoir utiliser correctement les divergences moléculaires comme indicateurs temporels.

Ces différents propos seront illustrés par une série d'exemples, concernant avant tout les Mammifères, et basés sur des phylogénies moléculaires acquises par différentes approches (séquençage, RFLP, hybridations ADN, électrophorèse). Ces arbres moléculaires seront confrontés à ceux dérivés de l'approche morphologique traditionnelle, et un compromis entre les deux approches pourra être dégagé.

R.I. Vane-Wright (London): Age and area revisited – problems with butterflies and island biogeography.

The relationship between the age of a particular natural group and its range size is not predictable. Modern representatives of ancient lineages can occupy very large areas (e.g. the almost cosmopolitan Libytheidae amongst the butterflies), or be restricted (e.g. the primitive swallowtail *Baronia*, in Mexico), while recent taxa can occupy five continents (e.g. the milkweed butterfly sister species pair, *Danaus gilippus* and *D. chrysippus*), or be very restricted (e.g. the danaine *Amauris nossima* in the Malagasy region). However, whilst it is true that many individual species have far wider ranges than particular genera, families or other higher taxa, there is a statistical relationship: the average range of species is necessarily less than that of genera, and that of genera less than families, and so on. This is so simply because the range of an individual genus can never be less than that of its most widespread included natural groups (lineages), the age and area of a higher group can never be less than that of its oldest included species or any subordinate taxon.

This seemingly trivial relationship of age and area, first discussed by the botanist J.C. Willis, can be used to investigate historical biogeography, even in the absence of rigorous knowledge of phylogenetic relationships. This is demonstrated by butterflies of the Malay Archipelago in relation to our understanding of the collision between the Australian and Asian tectonic plates. Ideas about age and area applied to the butterflies of Africa and Madagascar lead to speculations which could be tested by molecular investigations. Finally, the case of *Amauris comorana* is discussed: an apparently old species restricted to a small island considered to be no more than 120,000 years old. Such examples lead us to question existing phylogenetic and geological conclusions, and our ideas about the mode and tempo of evolution.

Marie-Claude Durette-Desset (Paris): The nematoda Trichostrongyloidea and their vertebrate hosts: an history lasting from the late secondary.

Reconstruction of the phylogenetic history of a parasitic group is clearly difficult due to a lack of fossil forms. Among the nematode parasites of vertebrates, the superfamily Trichostrongyloidea is one of the richest groups in terms of number of species (more than 1000 described) and genera (175) and they therefore offer excellent opportunities to reconstruct their phylogeny. Trichostrongyles occur in the gut and less commonly in the stomach and the lungs of all classes of terrestrial vertebrates except the Perissodactyls and the Proboscidiens. They have a world wide distribution and direct life cycle.

The criteria used in the classification of the Trichostrongyloidea are essentially morphological. Morphological characters are numerous and an attempt has been made to distinguish their relative value. Information concerning the synlophe, which is the apparatus of locomotion and attachment of the worms in the gut of the hosts, has been found essential in order to construct a classification of the superfamily and understand its evolution; thus the morphology of the synlophe has been studied and different phylogenetic lineages have been recognized. This analysis was greatly facilitated by information from two sources:

1. the morphology of the free-living rhabditids, which are the ancestors of the trichostrongyles. This has allowed us to determine the direction of evolution;

2. the ontogeny of the synlophe. The synlophe is often present in the fourth-stage larva and its form in the larva can be considered more primitive than that in the corresponding adult.

The results of this work show that there are three major groups within the Trichostrongyloidea, namely the "Trichostrongylids", the "Molineids", and the "Heligmosomids". In the first two groups, which are the most primitive, the synlophe is always bilaterally symmetrical as in most others nematodes. In the third group, which is the most evolved, the synlophe is never bilaterally symmetrical.

The classification established above takes account of the different morphological characters, but only concerns extant animals. Data provided by the hosts permit us to date the appearance of different lineages and to follow their evolution in time and space. These data come from extant hosts and from paleobiogeography.

1. The evidence from extant host species includes the host distribution of the trichostrongyles in relation to the geographic distribution of the hosts. Our analysis have revealed the following facts:

a. Each family or subfamily of trichostrongyles is characteristic of a group of hosts and/or a specific geographic region.

b. Host groupings, based on evidence from the worms, do not necessarily conform to zoological relationships of the hosts themselves.

c. The same parasite line can occur in the same hosts in the geographical regions which are widely separated from each other.

d. In contrast, the same group of hosts in the same geographical region can have different parasite lineages.

2. The evidence from extinct forms includes the date of appearance of the host in the geological record as well as mammalian migration in geologic time periods:

a. The date of the appearance of the hosts in the geological records permits us to date the origin of the different families of parasites. We postulate that if the host line remains stable, the parasite line will also remain stable. Thus, if an extant host morphologically resembles its ancestor from the Eocene, we may assume that the parasite in that host also resembles its ancestor from the Eocene and can therefore be dated to that epoch. This type of analysis has been carried out for the entire superfamily Trichostrongyloidea.

b. The manner in which host migration interacts with the parasite is very complex and a few examples will be consider, mainly from the caviomorphs, the sciurormorphs and the myomorphs.

The combination of evidence from the morphology of the worms and evidence from the paleobiogeography of the hosts allows us not only to explain the present day host and geographic distributions of the parasites but also to reconstruct their evolutionary history.

The phylogenetic tree of the Trichostrongyloidea proposed with Chabaud consists of three main branches which are morphologically clearly defined. Fourteen families of trichostrongyles can be distinguished, of which twelve are included in the three main groups. The other two are cosmopolitan families of little interest because they occur in birds and in rhynolophes. The distributions of the twelve families are remarkable because all of the most primitive forms and the majority (8) of the families occur in hosts which have a Gondwanian distribution. Four families are found in the Holarctic, i.e., the Trichostrongylidae, Molineidae, Heligmosomidae and Heligmonellidae. The Trichostrongylidae have spread around the world with the lagomorphs and ruminants. The latter three families spread to Laurasia and into the Eutheria by the way of insectivores (Tenrecoidea, Soricoida and Talpoidea).

According to our hypothesis, the Trichostrongyloidea appeared at the end of the Secondary. At the beginning of the Tertiary most families already existed. Evolution continued throughout the Tertiary and, in certain subfamilies is still occurring today.

The principal evolutionary process in the trichostrongyles and in nematodes in general is the phenomenon of host-switching, i.e. the nematode transfers from one host group to another and undergoes isolation and speciation. Speciation resulting from host-switching may be of little or great evolutionary significance. Host-switching is rendered possible by the presence of free ecological niches resulting from the evolution of new hosts or the migration of hosts into new localities. The type of association between the trichostrongyles and their hosts is therefore relatively loose but is explicable by the biology of the parasite.

SHORT PAPERS AND POSTERS

Bernard D. Flury, Jean-Pierre Airoidi and Jean-Pierre Biber (Bern): Gender identification of Water pipits (*Anthus spinoletta*) using mixtures of distributions.

Distributions with two distinct peaks, also called bimodal distributions, are a frequent phenomenon in biometrical studies. Such mixtures of distributions arise when a population consists

of more than one homogeneous class (or component), but the investigator does not know to which of the components any given specimen belongs. Mixture analysis is a modern statistical technique to deal with this situation; in particular, it attempts to estimate the statistical parameters (means and standard deviations) of each of the components, as well as their proportion in the population. A review of some basic concepts of mixture analysis is presented on a non-technical level and an illustration of the method is given using the wing length of Water pipits, the two components being males and females. Frequency plots of wing length show distinct bimodality which can be ascribed to sexual dimorphism, but the gender of each individual bird is not known. Mixtures of two normal distributions appear to be appropriate for modelling this situation.

Finally, differences between mixture analysis and related methods such as discriminant analysis or cluster analysis are also discussed.

François M. Catzeffis (Montpellier): Tempo and modes of speciation in the rodents Muridae (Mammalia): Molecules versus Morphology.

The Murinae, a possible monophyletic clade among 14 other subfamilies of the Muridae sensu lato, is the most successful taxon of the rodents, encompassing at least 115 genera in ca. 460 living species. The evolutionary systematics of this group of "rats and mice" is in a strong need of a synthetic effort including paleontological and neontological approaches, especially above the specific level.

Among the most recent results, the case of the genus *Mus* sensu lato is of interest: the living mice can be subdivided into four subgenera, one of them being exclusively African in Recent distribution. The branching pattern, based on DNA hybridization experiments, of the ca. 12 species so far studied is not only in rough agreement with classical morphological data, but clearly supports the monophyly of each subgenus. The molecular time scale, calibrated by fossil data pertaining to the history of *Mus*, *Apodemus*, *Antemus*[†], *Progonomys*[†] and *Rattus*, allows to date approximately each speciation event. Finally, the re-examination of the fossil record pertaining to both Asian and African *Mus* spp. re-inforces the temporal results of the molecular phylogeny.

M. Rowell-Rahier (Basel): Genetic distance between *Oreina* species (Chrysomelinae) with different defensive strategies.

Paper published elsewhere.

F. Saucy and A.-G. Wust Saucy (Lausanne): Genetical differentiation between fossorial and aquatic populations of *Arvicola terrestris*: preliminary results.

Paper published elsewhere.

M. Ruedi, M. Chapuisat (Lausanne) and **D.T. Iskandar** (Bandung): Genetic structure of the Lesser Gymnure (Genus *Hylomys*) in SE-Asia: evidence for two species.

The Lesser Gymnure is a small galericine Insectivore living in the mainland forests of Southeast Asia, including the major islands of Sumatra, Java and Borneo. It is the only representative of the supposed monospecific genus *Hylomys* which is morphologically rather constant over its geographic range. Only marginal subspecific differentiation is currently recognized based on slight pelage colour variations.

We report here the results of 35 gene loci revealed by protein electrophoresis on 23 specimens sampled over most of Southeast Asia. They were compared with an outgroup, *Erinaceus europeus*, member of a distinct subfamily. The surveyed populations of Lesser Gymnures clearly group themselves into two distinct taxa, one of which seems restricted to Sumatra, while the other occupies the whole geographic range. The genetic distance between these groups is two times greater than the

divergence observed within groups; it is of the same order of magnitude as what is usually reported for congeneric mammal species, which supports their specific distinction. The lack of gene flow is also demonstrated by several diagnostic loci defining unambiguously each species. Both are only distantly related to the outgroup, a result which is consistent with their actual classification into two distinct subfamilies (Erinacinae and Galericinae).

Concordant genetic and geographic subdivision of the widespread species further suggest that eustatic sea level changes during the Pleistocene produced predictable patterns in species differentiation.

Manfred Zimmermann (Berne) and **Christian P. Klingenberg** (Edmonton): Static, ontogenetic, and evolutionary allometry: a comparative multivariate morphometric study of the swiss waterstrider species (Hemiptera, Gerromorpha, Gerridae).

Paper published elsewhere.

I. Löbl (Genève): La diversité et la distribution des Scaphidiidae (Coleoptera) de l'Himalaya.

Paper published elsewhere.

S. Ingrisch (Zürich): Intraspecific variation of the grasshopper of the *Chortippus biguttulus* group in the alps (stridulation and morphology).

Paper published elsewhere.

D. Burckhardt (Genève): Host plant and biogeographic relationships of the Indo-Australian plant louse genus *Cecidopsylla* (Homoptera, Psylloidea).

Paper published elsewhere.

P. Cuénoud et **C. Lienhard** (Genève): Les psocoptères du bassin genevois.

Paper published elsewhere.

C. Vaucher (Genève): Le genre *Vampirolepis* (Cestoda), un casse-tête pour l'helminthologiste systématique.

Paper published elsewhere.

N. D. Springate (Genève): The cenchri of Symphyta.

Paper published elsewhere.

R. Desqueyroux-Faúndez et **D. Cambin** (Genève): Nouvelles données sur les Spongillides en Suisse Romande.

Paper published elsewhere.

Adolf Scholl (Berne) and **Ariane Pedrolí-Christen** (Neuchâtel): The genus *Rhymogona* (Diplopoda: Craspedosomatidae), a ring species? – Enzyme electrophoretic data.

Rhymogona is a small genus of the Diplopoda family Craspedosomatidae which comprises seven nominal species. This genus has a very restricted distribution, which extends north of the Swiss Alps to the Black Forest in the northeast and is limited from northwest to southwest by the Vosges,

Côte d'Or and Savoy. Several *Rhyogona* species are known from one or a few localities only. We have initially attempted to study the distribution in detail. Species identification in this genus is based essentially on subtle differences in morphology of genitalia, in several species of males only. Since identification is often not unambiguous, we have used enzyme electrophoresis to study the genetic differentiation of the taxa concerned, and we have asked if electrophoretic data might be used as additional information for species identification.

During these studies it became evident that we are dealing with a ring species which is distributed around the Swiss and French Jura. The electrophoretic analysis reveals five major groups of genetically differentiated populations. Adjacent groups of these populations differ by allele substitution in one out of twelve enzyme loci surveyed. Populations at the extremes are nominal *R. cervina* and *R. montivaga*, which differ by allele substitutions in four out of the twelve enzyme loci surveyed. These taxa come in contact in the Swiss Jura and in the Swiss Alps, where they form very narrow hybrid zones.

Remo Wenger, Hansjürg Geiger and Adolf Scholl (Berne): Electrophoretic evidence of hybridization of *Pontia daplidice* (Linnaeus, 1758) and *P. edusa* (Fabricius, 1777) (Lepidoptera: Pieridae) in a contact zone in northern Italy.

Our previous electrophoretic studies have indicated the existence of two genetically distinct parapatric taxa within the nominal *Pontia daplidice* (L.) in southern Europe. These taxa differ in allele substitutions at four out of 24 enzyme loci surveyed. Furthermore, analysis of adult morphology revealed differences in the shape of valvae and in the markings of the forewing underside, with slight overlap between both taxa. Laboratory studies indicated no premating but strong postmating barriers in crosses between specimens from France and Greece. Wagener (1988) ranked these taxa as semispecies. We showed that the western European taxon (*daplidice* L., sensu Wagener) flies in France, Spain, Morocco, Israel and Turkey, whereas the eastern European taxon (*edusa* Fabricius, sensu Wagener) is found in Switzerland, Italy, Austria, Yugoslavia, Hungary, Greece and Turkey.

We continued our studies on the distribution of both taxa, with particular emphasis on detecting contact zones. The new data (40 collecting sites in northwestern Italy, 461 specimens) demonstrate that *P. daplidice* extends its range east beyond the Alpes Maritimes into northern Italy. Both taxa meet north of the Ligurian Alps. In a rather narrow hybrid zone south of Alexandria most samples contained both taxa. There were no F_1 -hybrids among more than 300 butterflies from this area, however, most samples contained a fraction (10-30%) of back-cross hybrids. In spite of the fact that these butterflies are considered medium distant migrants, there was no gene flow observed beyond the hybrid zone.